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COMPOSITION AND STRUCTURE OF AN EASTERN AMAZONIAN FOREST AT CAMAIPI, AMAPA, BRAZIL

Scott A. Mori[1], Benedito V. Rabelo[2]
Chih-Hua Tsou[1] and Douglas Daly[1]

ABSTRACT – A forest inventory, based on a sample of 1000 trees 10 cm or more in diameter, was carried out in eastern Amazonian Brazil at Camaipi, Amapá. The Camaipi forest is located in the Amazon Basin on sedimentary deposits about 45 km N of the present-day Amazon River. Individual trees display the reverse J-shape size class distribution and have an average size of 643.6 cm^2*. There are 546. trees per hectare and a dominance of 35.1 m*^{2} *per hectare.* Geissospermum argenteum *is by far the most frequent, common, and dominant species. Its Importance Value of 51.1 is among the highest recorded for a non-flooded neotropical forest. Moreover, the predominance of trees of this species in the 30-39 cm size class interval and the high average tree size of 942.6 cm*^{2} *indicate that some event within the last several hundred years promoted its establishment. Because of the abundance of* G. argenteum, *the Apocynaceae ranks as the most important family of trees in the Camaipi forest. Other important families are the Sapotaceae, Mimosaceae, Burseraceae, Lecythidaceae, Caesalpiniaceae, Chrysobalanaceae, Melastomataceae, and Lauraceae. Although diversity is high, it is lower than a comparable forest on the Precambrian Guayana Shield at Saül, French Guiana. The possible causes of the lower species diversity at Camaipi are discussed.*

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[1] The New York Botanical Garden, Bronx, Ney York 10458-5126.

[2] Museu Ângelo Moreira da Costa Lima, Centro de Pesquisas Zoobotânicas, Rodovia Juscelino Kubstichek, Km 10-Fazendinha, Macapá, Amapá, Brasil.

KEY WORDS: Forest inventory, Phytosociology, Forest Structure.

RESUMO – Um inventário florestal, baseado numa amostragem de 1000 árvores com diâmetros de 10 centímetros ou mais, foi efetuado para uma mata na Bacia Amazônica oriental na localidade de Camaipi, Amapá. Essa mata está situada a cerca de 45 km ao N do rio Amazonas sobre depósitos sedimentares. As árvores mostram uma distribuição de "J" em reverso para as classes de tamanho e uma área basal média de 643,6 cm^2*. Essa mata tem 546 árvores/hectare e uma área basal total de 35,1 m*^{2}*/hectare.* Geissospermum argenteum *é a espécie mais freqüente, comum, e dominante. Seu valor de importância de 51,1 está entre os mais altos índices reportados para uma mata neotropical de terra firme. A predominância de árvores desta espécie na classe de 30 a 39 cm de diâmetro e o alto valor médio de área basal de 942,6 cm*^{2} *indica que algum evento nos últimos duzentos anos tem favorecido o estabelecimento desta espécie. Devido à alta importância de* G. argenteum, *a Apocynaceae é a mais importante família de árvores na mata de Camaipi. Outras famílias importantes são Sapotaceae, Mimosaceae, Burseraceae, Lecythidaceae, Caesalpiniaceae, Chrysobalanaceae, Melastomataceae, e Lauraceae. Embora a diversidade de espécies de árvores na mata de Camaipi seja alta, ainda assim é mais baixa do que a diversidade de uma mata sobre o Escudo das Guianas em Saül, Guiana Francesa. As possíveis razões pela relativa baixa diversidade da mata de Camaipi são discutidas.*

PALAVRAS-CHAVE: Inventário florístico, Fitossociologia e Estrutura da floresta.

INTRODUCTION

Quantitative ecological studies of the forests of the vast Amazonian hylaea began in Amazonian Brazil with the study of Black et al. in 1950. Their work, stimulated by the studies of Davis and Richards (1933, 1934) in Guyana (then British Guiana), has promoted a series of papers on the forest vegetation of Amazonian Brazil (Bastos, 1960; Cain et al., 1956; de Carvalho, 1980, 1981; Dantas et al., 1980; Klinge & Rodrigues, 1968; Magnanini, 1952; Pires & Koury, 1958; RADAM, 1974; Rodrigues, 1962). A review of ecological studies throughout Amazonia is provided by Daly and Prance (1989). These studies have demonstrated that: (1) the forests of Amazonian Brazil are rich in species; (2) species composition and diversity changes drastically from one site to another; (3) a relatively few species account for most of the importance value of a given forest; and (4) many species are represented by one or fewer individuals per hectare. Moreover, these studies provide data on the density, frequency, dominance, and diversity of the species of trees studied.

A pioneer study of the phytogeography of the Amazon Basin is that of Ducke and Black (1954). They demonstrate that the flora of eastern Amazonian Brazil has been, and continues to be, influenced by the Amazon River. They point out that species diversity appears to be lower in eastern than in central and western Amazonia. They also suggest that species composition north and south of the Amazon River is more divergent in eastern Amazonia than it is in western Amazonia.

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The purpose of this paper is to describe a non-inundated forest of the Amazonian floodplain and compare it with other neotropical forests, especially one located at Saül, French Guiana on the Guayana shield.

STUDY SITE

This inventory was carried out from September to October, 1983 and in December, 1984 at Camaipi, Amapá (O°10'N,0°, 51°37'W) which is located about 30 km NW of Mazagão. The transects were located in a 2,380 hectare reserve of the Empresa Brasileira de Agropecuária (EMPRABA). Although the reserve is currently protected from the rampant deforestation taking place around it, there is no guarantee that it will remain protected because all or part of it may be utilized in the future by EMBRAPA for agricultural experimentation.

The territory of Amapá can be divided into two distinct geological regions. The Precambrian Guayana Shield which occupies the vast majority of the territory and the smaller sedimentary areas which fringe the Atlantic coast and the north bank of the Amazon River. The sedimentary areas were deposited in the late Tertiary and the Pleistocene (Fittkau, 1974; Guerra, 1952). Camaipi is located on the sedimentary deposits about 45 km N of the Amazon River. The study site itself is situated on a low plateau at less than 100 m elevation and is generally of low topographic relief. It is dissected only by occasional small streams. The interfluvial areas are nearly flat, broad plateaus.

The Camaipi site is covered by non-inundated (*terra firme*) forest and therefore species diversity is not limited by periodic excesses of soil moisture. To the east and southeast this forest is bordered by savanna (*campo*), to the north and west by other *terra firme* forests, and to the south by periodically inundated or *várzea* forest.

Annual yearly rainfall is on the order of 2,500 mm (Nimer, 1977) and there is a marked dry season beginning in July and ending in December (Salati, 1985).

The transects were placed in *terra firme* forest. The soils at the study site are acidic, ranging from 4.8-4.9 pH. Phosphorous occurs in 1 p.p.m. and potassium ranges from 6-16 p.p.m. Calcium and magnesium are present in 0.8-1.1 mil equivalents, the percent nitrogen ranges from 0.13-0.25, the percent carbon from 1.24-2.88, and the percent organic material from 2.13-4.95. The range of values depends on the location and depth of the sample.

METHODS

One thousand trees with diameters at breast height (DBH) equal to or greater than 10 cm were sampled using the point-centered quarter method of Cottam and Curtis (1956). Five separate transects, totalling 5000 meters in length, were established at azimuths of 140°. The transects were parallel and separated from one another by 1000 meters. The sample points along the lines were placed 20 m apart. The sampling method and analysis of data follows that described in more detail by Mori et al. (1983a).

The trees were marked with numbered aluminum tags and were revisited the following year to gather data on mortality, to fill in missing data, and to collect additional specimens for trees not properly vouchered. Herbarium collections were gathered for all trees for which there was any doubt in identification. However, easily identifiable trees were also collected at least once. Tree and voucher numbers for the species are provided in Table 1. A complete set of voucher collections is deposited in the herbarium of the Museu Amapaense (HAMAB) and a list of all species and their vouchers is available from the senior author. Only a limited set of voucher collections is deposited at NY.

Table 1 – Tree and voucher numbers for species discussed in the text. The tree number appears in parentheses and is followed by the collection number in the series of S. Mori.

Anacardiaceae
Thyrsodium guianense Sagot ex March.
(2009) 15800; (2197) 15290; (2215) 15934.

Apocynaceae
Geissospermum argenteum Woods.
(2001) 15798.
Aspidosperma carapanauba Pichon
(2128) 15880; (2162) 15895; (2264) 15964; (2336) 16019; (2651) 16243.
A. macrocarpon Mart.
(2951) 16453.

Boraginaceae
Cordia exaltata Lam.
(2010) 15801; (2029) 15816A; (2031) 15818; (2072) 15842.

Burseraceae

Protium firmum Swart

(2110) 15866; (2111) 15867; (2121) 15875; (2216) 15935; (2266) 15965; (2311) 16000; (2312) 16001; (2381) 16050; (2421) 16095; (2465) 16122; (2532) 16160A; (2543) 16166 (2644) 16239; (2699) 16271.
P. tenuifolium (Engl.) Engl.
(2018) 15808; (2339) 16021; (2348) 16027; (2412) 16093; (2493) 16138; (2497) 16141; (2508) 16147; (2516) 16150; (2538) 16162; (2561) 16182; (2579) 16198; (2585) 16202; (2592) 16205; (2608) 16217; (2610) 16219; (2619) 16225; (2625) 16230; (2632) 16233; (2643) 16238; (2652) 16244; (2671) 16259; (2682) 16262; (2703) 16274; (2704) 16275; (2766) 16314; (2777) 16324; (2822) 16369; (2833) 16377; (2839) 16381; (2844) 16383; (2892) 16410; (2927) 16434; (2994) 16483.
Tetragastris panamensis (Engl.) O. Ktze.

(2017) 15807; (2050) 15828; (2093) 15856; (2167) 15898; (2170) 15900; (2188) 15913; (2272) 15968; (2280) 15974; (2316) 16004; (2342) 16023; (2474) 16125; (2524) 16155; (2607) 16216; (2658) 16250; (2701) 16273; (2719) 16285; (2721) 16287; (2722) 16288; (2724) 16289; (2793) 16350; (2859) 16391; (2888) 16407; (2890) 16409; (2900) 16416; (2928) 16435; (2948) 16450; (2966) 16462; (2972) 16467; (2982) 16473.

Caesalpiniaceae
Tachigalia myrmecophila Ducke
(2020) 15180; (2126) 15880A; (2179) 15907; (2201) 15923.

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continued

Table 1 – continuation

T. alba Ducke
(2043) 15824; (2083) 15849; (2287) 15979; (2435) 16103; (2788) 16346; (2826) 16373; (2964) 16460.

Humiriaceae
Saccoglottis guianensis Benth.
(2150) 15890; (2332) 16017; (2452) 16113; (2536) 16161; (2759) 16308; (2791) 16348; (2824) 16371; (2902) 16417; (2919) 16429; (2930) 16437.

Lauraceae
Nectandra amazonum Nees
(2054) 15832; (2102) 15861; (2117) 15872; (2130) 15882; (2156) 15893; (2166) 15897; (2178) 15906; (2302) 15994; (2432) 16101; (2618) 16224; (2675) 16261; (2691) 16266; (2720) 16286; (2739) 16297; (2767) 16315.

Lecythidaceae
Lecythis persistens Sagot
(2214) 15933; (2361) 16039; (2386) 16054; (2438) 16104; (2604) 16213; (2641) 16237; (2653) 16245; (2662) 16254; (2664) 16255; (2668) 16258; (2672) 16260; (2874) 16399.
Lecythis poiteaui Berg
(2124) 15878.

Melastomataceae
Miconia punctata (Desr.) Don
(2310) 15999; (2315) 16003; (2354) 16032; (2597) 16207; (2617) 16223; (2665) 16256; (2693) 16268; (2713) 16282.
Mouriri torquata Morley
(2012) 15803; (2101) 15860; (2233) 15942; (2256) 15959; (2366) 16041A; (2407) 16090; (2433) 16102; (2460) 16119; (2525) 16156; (2533) 16160 (2629) 16231; (2775) 16322; (2823) 16370; (2825) 16372; (2926) 16433.

Mimosaceae
Dinizia excelsa Ducke
(2639) 16236; (2846) 16385; (2877) 16401; (2889) 16408.
Pithecellobium racemosum Ducke
(2296) 15985; (2372) 16043; (2403) 16086; (2602) 16211; (2667) 16257; (2753) 16304; (2817) 16366; (2829) 16374.

Myristicaceae
Virola michelii Heckel
(2051) 15829; (2122) 15876; (2142) 15887; (2171) 15901; (2189) 15914; (2258) 15960; (2352) 16030; (2405) 16088; (2486) 16133; (2539) 16163; (2545) 16168; (2577) 16196; (2661) 16253; (2728) 16292; (2734) 16294; (2769) 16317; (2773) 16321; (2794) 16351; (2807) 16361; (2896) 16413; (2984) 16475.

Ochnaceae
Ouratea discophora Ducke
(2106) 15864; (2109) 15865; (2112) 15868; (2113) 15869; (2120) 15874.

Sapotaceae
Franchetella anibaefolia (A. C. Smith) Aubr.
(2039) 15823; (2074) 15843; (2165) 15896; (2173) 15903; (2411) 16092; (2551) 16174; (2740) 16298; (2771) 16319; (2782) 16342; (2944) 16447; (2965) 16461.

continued

Table 1 – conclusion

F. gongrijpii (Eyma) Aubr.
(2076) 15845; (2289) 15980; (2331) 16016; (2337) 16020; (2392) 16057; (2442) 16106; (2522) 16153; (2555) 16176; (2575) 16189; (2606) 16215; (2609) 16218; (2624) 16229; (2654) 16246; (2957) 16456; (2958) 16457.
Manilkara amazonica Huber
(2153) 15892; (2347) 16026; (2694) 16269; (2708) 16278; (2838) 16380; (2394) 16411; (2946) 16449; (2978) 16471; (2987) 16477; (2990) 16480.
M. huberi (Ducke) Chevalier
(2006) 15797; (2049) 15827.
Pouteria sagotiana (Baill.) Eyma
(2026) 15815; (2077) 15846; (2131) 15883; (2186) 15911; (2200) 15922; (2353) 16031; (2380) 16049; (2382) 16051; (2485) 16132; (2698) 16270; (2736) 16295; (2737) 16296; (2750) 16302; (2772) 16320; (2781) 16341; (2785) 16345; (2936) 16442; (2961) 16459; (2971) 16466.

Species concepts were first established by studying the voucher collections while still in the field. This allowed us to solve species problems by returning to examine the numbered trees. Duplicates of the voucher specimens were then sent to specialists for identification or matched by the two senior authors in the herbaria of the Museu Goeldi (MG) or The New York Botanical Garden (NY).

Distance to Nearest Conspecific (DNC) measurements were made for eleven readily identifiable trees. The number of trees per species ranged from five (*Dinizia excelsa* Ducke) to 182 (*Geissospermum argenteum* Woods.). Only nearest conspecifics 10 cm or greater were included in the sample.

The data of this study were compared with that gathered from three other studies in which similar methods were employed. These other studies are based on work in Amazonian Ecuador (Balslev et al., 1987), eastern extra-Amazonian Brazil (Mori et al., 1983a), and the Guayana Shield of French Guiana (Mori & Boom, 1987).

RESULTS

Size. The trees of Camaipi display the reverse J-shape or negative exponential distribution characteristic of most forests (Figure 1). The percent of trees per 10 cm size class interval is: 10-19 (52.9%), 20-29 (22.5%), 30-39 (11.6%), 40-49 (6.1%), 50-59 (2.8%), 60-69 (1.7%), 70-79 (1.4%), 80-89 (0.4%), 90-99 (0.3%), 100-109 (0.1%), 110-119 (0.2%). The average basal area per tree 10 cm or greater DBH at camaipi is 643.6 cm^2 (Table 2). The size class distribution of *Geissospermum argenteum* differs markedly from that of the overall forest. There are many fewer trees in the 10-19 cm interval (Figure 1) and the average basal area per tree of 942.6 cm^2 of this species is much larger.

Frequency. In order to calculate frequency, five consecutive points were combined to make a single sampling unit, i.e., points 1-5 = sampling unit 1; points 6-10 = sampling unit 2; and so forth. In this way 250 points yielded 50 sampling units. The presence of each species was recorded each time it appeared in a sampling unit. The 205 species found in the 1000 tree sample gave 734 occurrences. The absolute frequency of a species is the number of sampling units in which it occurs, whereas the relative frequency is the total number of occurrences of a given species divided by 734.

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Table 2 – Sample size, tree densities, average basal area/tree, total basal area/hectare, and nº trees/species in four lowland, neotropical forests. Includes all trees 10 cm or greater in diameter. The data were gathered using the point-centered quarter sampling method.

Locality	Sample Size (no. trees)	Density (trees/ hectare)	Average Basal Area/ tree (cm^2)	Basal Area/ hectare (m^2)	No. Species/ 800 trees
Añangu (Balslev et al. 1987)	800	728	462.9	33.7	244
Bahia (Mori et al., 1983)	600	819	519.1	46.3	–
Saül (Mori & Boom, 1987)	800	619	856.7	53.0	295
Camaipi	1,000	546	643.6	35.1	188

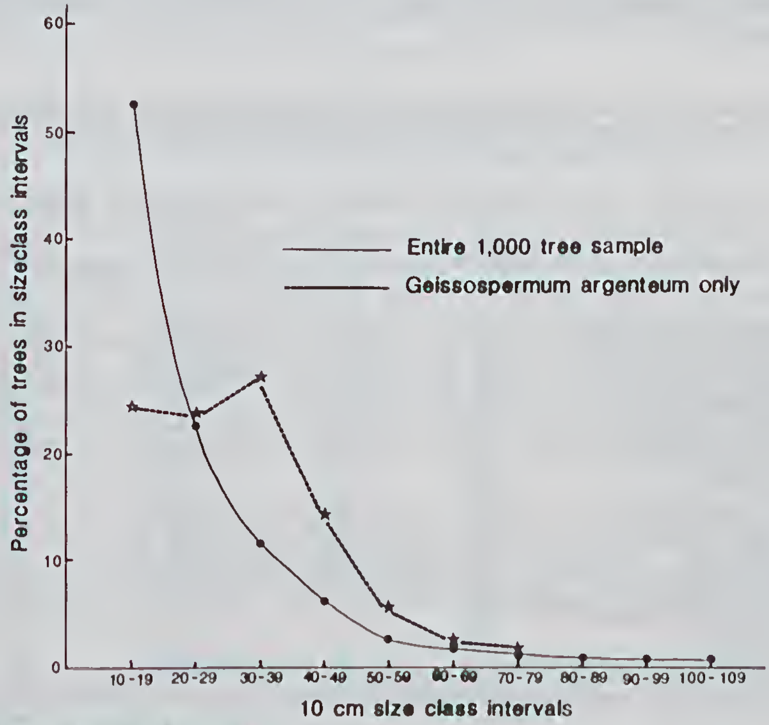

Figure 1 – Tree size class distribution.

The most frequent species is *Geissospermum argenteum* which occurred in 44 out of the 50 (88%) sampling units. This species is found throughout the entire forest. An additional 13 species were found in 25% or more of the sampling units (Table 3). These species are: *Tachigalia myrmecophila* Ducke (27 occurrences), *Protium tenuifolium* (Engl.) Engl. (22), *Tetragastris panamensis* (Engl.) O. Kuntze (22), *Virola michelii* Heckel (19), *Lecythis persistens* Sagot (18), *Pouteria sagotiana* (Baill.) Eyma (16), *Thyrsodium guianense* Sagot ex March. (16), *Manilkara amazonica* Huber (13), *Mouriri torquata* Morley (13), *Protium firmum* Swart (13), *Nectandra amazonum* Nees (13), *Franchetella gongrijpi* (Eyma) Aubr. (12), and *Miconia punctata* (Desr.) Don (12).

Density. There are 546 trees equal to or greater than 10 cm DHB per hectare at Camaipi. *Geissospermum argenteum,* with a relative density of 18.3% and an absolute density of nearly 100 trees per hectare, is by far the commonest species. The next most common, *Lecythis persistens,* has a relative density of 4.9% and an absolute density of 26.8 trees per hectare (Table 3). Ninety-five of the 205 species have absolute densities of only one tree per hectare.

Dominance. Average tree size of the 1,000 tree sample is 643.6 cm^2. This yields a total basal area for the 546 trees per hectare equal to or greater than 10 cm DBH of 35.1 m^2/hectare. *Geissospermum argenteum,* with a relative dominance of 26.8% and an absolute dominance of 9.4 m^2, is by far the most dominant species in the Camaipi forest. Other species with high dominance values are listed in Table 3.

Table 3 – Twenty-five most important tree species the forest of Camaipi. Values are given for the 1.000 trees greater than or equal to 10 cm DBH sampled, not per hectare.

Species	No. Occurrences	No. Trees	Basal area (cm^2)	Importance Value
Geissospermum argenteum	44	183	172,504.7	51.1
Tachigalia myrmecophila	27	44	35,264.6	13.5
Tetragastris panamensis	22	29	26,530.0	10.0
Lecythis persistens	18	49	9,288.7	8.8
Protium tenuifolium	22	34	11,496.4	8.2
Manilkara amazonica	13	15	23,784.6	7.0
Virola michelii	19	23	8,515.6	6.2
Pouteria sagotiana	16	20	11,107.5	5.9
Thyrsodium guianense	16	19	7,909.3	5.3
Tachigalia alba	11	12	13,384.2	4.8
Mouriri torquata	13	15	7,544.2	4.4
Aspidosperma carapanauba	7	8	17,299.3	4.4
Dinizia excelsa	5	5	18,143.9	4.0
Aspidosperma macrocarpon	6	6	16,016.3	3.9

continued

Table 3 – conclusion

Species	No. Occurrences	No. Trees	Basal area (cm^2)	Importance Value
Nectandra amazonum	13	15	3,601.2	3.8
Protium firmum	13	15	3,178.1	3.8
Franchetella anibaefolia	10	12	7,145.1	3.7
Manilkara huberi	7	8	11,523.4	3.5
Pithecellobium racemosum	11	11	5,887.9	3.5
Franchetella gongrijpi	12	15	2,111.9	3.5
Lecythis poiteaui	7	9	9,493.7	3.3
Miconia punctata	12	13	2,362.4	3.3
Saccoglottis guianensis	9	10	6,371.1	3.2
Ouratea discophora	9	16	2,237.6	3.2
Cordia exaltata	11	13	1,696.7	3.1

Importance Values. Importance values (IV) were calculated by adding the relative frequency, relative density, and relative dominance of each species (Curtis & Cottam, 1962). The IV of a species gives an indication of (1) how frequently it is encountered throughout the forest (relative frequency), (2) how abundant it is (relative density), and (3) how large its individuals are (relative dominance). Therefore, the sum of these values is an indication of the overall importance of a given species in a community.

By far the most important species at Camaipi is *Geissospermum argenteum* with an IV of 51.1. The 25 most important species at Camaipi are listed in Table 3. These 25 species account for 58.5% of the 300 point IV index.

Family Importance Values Using Cronquist's (1981) system of classification, a total of 47 families of plants were found in the 1000 tree sample. Only seven individuals were not placed to family and five of these were legumes that belong to either the Caesalpiniaceae or the Fabaceae (Table 4). In order to evaluate which of these families are most important at Camaipi, we used the Family Importance Value (FIV), which is the sum of the relative diversity, the relative density, and the relative dominance for all individuals of the family in the sample (Mori et al., 1983b). The Apocynaceae (FIV=57.8), Sapotaceae (30.1), Mimosaceae (24.9), Burseraceae (20.8), and Lecythidaceae (18.2) are the five most important tree families at Camaipi. The 30 most important families are listed in Table 4.

Diversity. A total of 205 species was encountered in the 1000 tree sample. One hundred and eighty-eight species appeared among the first 800 trees sampled. Diversity in the 800 trees sample was calculated in order to allow comparison with other 800 trees samples from Añangu, Ecuador and Saül, French Guiana.

Spatial patterns. Of the 11 species examined in the Distance to Nearest Conspecific (DNC) analysis, all but *Manilkara huberi* (Ducke) Chevalier haver a clumped distribution (Table 5).

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Mortality. Fourteen months after the 1000 trees sample was initially marked, only 11 trees had died. Six of these trees were still standing, whereas five had their trunks snapped in one way or the other. One of the latter, with its trunk broken 2 m from the ground, had its trunk filled with a termite nest. The other four had probably been broken by adjacent tree falls. A few other trees were nearly uprooted or had resprouted from broken trunks but these were not included in the mortality census because they were still alive.

Table 4 – Thirty leading tree families of Camaipi. Based on Family Importance Value (FIV) for the 1000 trees sample.

Family	No. Trees	Basal Area (cm^2)	No. Species	FIV
Apocynaceae	207	213,622.4	8	57.8
Sapotaceae	99	67,833.5	20	30.1
Mimosaceae	57	57,649.2	21	24.9
Burseraceae	88	49,123.0	9	20.8
Lecythidaceae	80	37,267.9	9	18.2
Caesalpiniaceae	63	51,294.8	7	17.7
Chrysobalanaceae	40	13,129.8	14	12.8
Melastomataceae	45	13,888.0	10	11.5
Lauraceae	39	12,403.0	10	10.7
Fabaceae	18	14,416.1	11	9.4
Annonaceae	15	5,413.2	9	6.7
Anacardiaceae	30	10,720.4	4	6.6
Myristicaceae	26	9,541.7	5	6.5
Myrtaceae	22	2,600.1	7	6.0
Rubiaceae	6	7,811.9	4	3.8
Ochnaceae	18	2,747.8	3	3.7
Moraceae	6	4,802.2	4	3.3
Vochysiaceae	5	8,516.7	2	2.8
Boraginaceae	14	1,817.4	2	2.7
Hugoniaceae (= Linaceae)	5	10,075.0	1	2.6
Combretaceae	7	5,476.7	2	2.5
Malpighiaceae	10	3,390.1	2	2.5
Humiriaceae	10	6,371.1	1	2.5
Quiinaceae	6	1,348.6	3	2.3
Legumes	5	4,225.9	2	2.1
Clusiaceae	4	1,429.9	3	2.1
Celastraceae	5	3,508.7	2	2.0
Euphorbiaceae	3	927.2	3	1.9
Arecaceae	6	2,077.5	2	1.9
Meliaceae	6	1,255.4	2	1.8
Remaining families	55	18,922.8	23	19.9
Total	1,000	643,608.0	205	300.0

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DISCUSSION

The forest at Camaipi is comparable to other tropical forests (Table 2; Gentry, 1982a; Herwitz, 1981) in number of trees equal to or greater than 10 cm DBH per hectare (546), in average tree size (643.6 cm^2), dominance (35.1 m^2), and in the J-shape or negative exponential distribution of its tree size classes.

The extremely high Importance Value of 51.1 for *Geissospermum argenteum* is unusual for non-flooded tropical forests without edaphic restrictions. Pires (pers. comm.), however, reports that this species is common in many other areas of eastern Amazonian Brazil. Importance Values ranging from 12.5 (Myrtaceae indet. 17; Mori et al., 1983a), 23.4 (*Vochysia quianensis* Aubl.; Cain et al., 1956), 27.1 (*Iriartea deltoidea* R. & P.; Balslev et al., 1987), 27.3 (*Scheelea* sp., Balslev et al., 1987) to 28.7 (*Mabea brasiliensis* Muell. Arg.; Silva, 1980) have been calculated for other comparable neotropical forests. An IV of 54.7 has been registered for *Mollia lepidota* Spruce ex Benth. from a periodically inundated forest along the Rio Xingu (Campbell et al., 1986). However, if there are edaphic limiting factors at Camaipi, they are not apparent.

Hectare samples of trees from moist tropical forests with no soil limitations will usually include representatives from ca. 40 to 50 families when Cronquist's (1981) system of classification and a minimum tree diameter of 10 cm are used as standards. The Camaipi sample included 47 families among the 1000 trees surveyed. Previous studies have shown that the Arecaceae, Bombacaceae, Burseraceae, Caesalpiniaceae, Chrysobalanaceae, Euphorbiaceae, Fabaceae, Lauraceae, Lecythidaceae, Meliaceae, Mimosaceae, Moraceae, Myristicaceae, Myrtaceae, Sapotaceae, and Vochysiaceae are usually the most important families of trees in lowland, moist, neotropical forests (Balslev et al., 1987; Cain et al., 1956; Dansereau, 1947; Davis and Richards, 1934; Fanshawe, 1954; Gentry, 1982a; Grubb et al., 1963; Maas, 1971a, 1971b; Mori et al., 1983a, 1983b, 1987; Prance et al., 1976, Sabatier, 1985; Schulz, 1960; Silva, 1980; Takeuchi, 1962; Veloso, 1946). The Apocynaceae, with the highest Family Importance Value of all families at Camaipi (57.8), now has to be added to this list.

Our 1000 tree sample was laid out along transects that covered five kilometers in length. Therefore, the total number of species sampled in comparison to a similar number of trees sampled in linear or square quadrats is expected to be greater (Mori & Boom, 1987). It is also important to understand that diversity values obtained with the point-centered quarter method can not be converted to absolute diversity per hectare. Consequently, the diversity figures for Camaipi can only be compared with those obtained in studies in which the same number of trees was sampled by the point-centered quarter method with the sample points spaced 20 m apart (Tabela 2). In comparison with the diversity data from Añangu and especially Saül, the presence of 188 species among the first 800 trees indicates relatively low diversity. In contrast, 295 species were found in the 800 trees sample from Saül.

It has been documented that tree species diversity varies considerably at different sites in the Neotropics. Counts of trees equal to or greater than 10 cm DBH on 1-ha plots in Amazonia have yielded values as low as 87 (Pires, 1957) and as high as 300 (Gentry, 1986a) different species. Several explanations may account for this vast difference in three species diversity. In the first place, forests on soils with limiting factors are known to possess fewer species per unit area than forests on soils without limiting factors. For example, in a study of a Guyanan forest, Davis and Richards (1934) recognized five different vegetation types, which they attributed to differences in soil moisture and organic content. Their extreme cases, the "Mora" forest association, which occurs on highly organic soils that never dry out, and the "Wallaba" forest association, which is found on white sand soils that rapidly dry out in the dry season, showed least species diversity. Pires and Koury (1958) and Campbell et al. (1986) have demonstrated that eastern Amazonian non-flooded forest is richer in species than periodically inundated (*várzea*) forest. The well-drained soils at Camaipi have no apparent edaphic limitations to species diversity.

Greater topographic relief may also promote species diversity. The influence of the Andes in providing opportunities for plant speciation has recently been emphasized by Gentry (1982b). However, even less dramatic changes in relief can increase species diversity by providing greater habitat diversity. For example, in a study of the ecology of neotropical Lecythidaceae, Mitchell and Mori (1987) have shown that certain species prefer ridge tops while others prefer valley bottoms. Of the study areas listed in Table 2, the Camaipi forest has the least topographic relief and, therefore, its low tree species diversity may be partially explained by fewer oportunities for niche specialization.

Eastern Amazonian botanists generally agree that lower species diversity, as well as dominance by fewer species, prevails in the early successional stages of Amazonian forests (Pires, pers. comm.). Saldarriaga (1987) has demonstrated that fewer species and lower biomass characterize secondary forests up to 80 years after shifting cultivation in Venezuelan Amazonia. The extremely high importance value of *Geissospermum argenteum* (Table 3), along with the disproportionately high number of trees in the larger size intervals of this species, suggest that some disturbance event promoted its establishment within the last several hundred years. If true, the lower tree species diversity of the Camaipi forest may be partially explained by the relative immaturity of this forest. The relatively high Family Importance Value of the Melastomataceae (Table 4), a family more common in secondary than mature forests, supports this hipothesis. Nevertheless, some primary forest species (e.g., *Dinizia excelsa, Manilkara huberi,* and *Pithecellobium racemosum* Ducke) are present.

Species diversity may also be related to the abundance and distribution of rainfall. Gentry (1982a) points out that wetter neotropical forests generally have more diverse plant communities than do drier ones. However, he has recently suggested that rainfall beyond 4000 mm per year is not accompanied by an increase in plant species diversity (Gentry, 1986b). The distribution of rainfall throughout the year also has to be taken into consideration. Nevertheless, the Camaipi forest has a dry season and rainfall regime comparable to that of the Saül forest, yet the latter forest is 1.6 times richer in species (Table 2).

Climatic changes that have taken place throughout geological time may have a considerable impact on species diversity. For example, the contraction of neotropical forests into refugia during glacial periods of the Pleistocene is thought by many to promote speciation (Prance, 1982a and papers therein). Acoording to this theory, tree species diversity is expected to be greater in areas of former refugia or at zones of contact between species that were formerly isolated in different refugia. The Camaipi forest does not coincide with any of the areas hypothesized as refugia for woody angiosperms by Prance (1982b). In contrast, the species rich forest at Saül is found in the eastern Guiana refuge (Prance, 1982b).

Finally, the past and present extent of the Amazon River may have greatly influenced species diversity at Camaipi. Ducke and Black (1954) have shown how the Amazon River in eastern Amazonia has restricted latitudinal migration of plants, whereas the same has not occurred in western Amazonia. Camaipi is located on recently deposited sedimentary rocks of the Amazon basin and was most certainly flooded throughout much of the Tertiary and Quaternary (Fittkau, 1974). Consequently, the Camaipi forest has a much shorter evolutionary past than, for example, the forest on the Precambrian Guayana Shield at Saül.

Our analysis of the distribution patterns of 11 selected trees species at Camaipi indicates that 91% of the species have clumped distributions (Table 5). This confirms the results of Armesto et al. (1986), Hubbell (1979), and Mitchell and Mori (1987) which suggest that many species of trees in tropical forest have clumped distributions.

Table 5 – Distance to nearest conspecific (DNC) Analysis for Camaipi. All trees greater than or equal to 10 cm DBH^3.

Species	No. of Trees	DNC (m)	Variance to Mean Ratio	Index of Dispersion	Probability Value
Geissospermum argenteum	181	6.94	1.60	293.80	.005 clumped
Lecythis persistens	49	7.47	5.71	274.10	.005 clumped
Tachigalia myrmecophila	43	10.04	2.46	103.40	.005 clumped
Protium tenuifolium	29	12.96	4.78	133.84	.005 clumped
Thyrsodium guianense	19	11.79	5.64	101.52	.005 clumped
Ouratea discophora	16	11.32	2.14	32.1	.005 clumped
Cordia exaltata	13	13.33	7.60	91.2	.005 clumped
Miconia punctata	11	22.17	5.69	56/95	.005 clumped
Manilkara huberi	8	26.67	1.49	10.46	NS random
Aspidosperma carapanauba			6.50	45.97	.005 clumped
Dinizia excelsa	5	22.64	4.55	18.2	.005 clumped

Hartshorn (1978) has demonstrated the frequent occurrence of tree falls in neotropical forests. In one of the lowland Costa Rican forests he studied, Hartshorn calculated a turnover time of 118 ± 27 years. Turnover time of the Camaipi forest is comparable to that calculated by Hartshorn. In a 14 month period 1.1% of the trees equal to or greater than 10 cm DBH at Camaipi had died. This gives a crude estimate of a turnover time of 90 years.

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